MUTATION IN PLANTS.[1]

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It is presumably safe to say that all students of natural history agree in the opinion that living matter has qualities at the present time that it did not originally, or always possess, and furthermore it is universally conceded that protoplasm is undergoing such development that it is constantly acquiring new properties, and taking form in an increasing number of types, kinds, or species of organisms as a consequence. In other words living matter is increasing the number of its qualities, multiplying the number of forms in which these qualities are variously grouped, and at the same time undergoing such differentiation that an increasing complexity is the general tendency of the organic world. These facts once realized the biologist finds himself confronted with two stupendous interrogatories. By what method is the general development and differentiation of organisms brought about as expressed in the formation or origin of new species, and secondly what are the general factors which shape this progression? The amount of mere discussion ensuing from the presentation of conflicting views brought out by these questions, in comparison with the total scientific effort to obtain positive evidence upon the points involved is appalling to contemplate. Happily the biological world is becoming intolerant of wrangling and speculative contentions, and has earnestly set about finding the facts that will afford an adequate and satisfactory solution to the main problems. The cult of the study of statistical variations may be regarded as one expression of this newly assumed attitude, while the devious, intricate and oft-times labyrinthine ways of cytological investi-

[1] The general discussion of the mutation theory embodied in this paper, together with an exhibition of the seedlings of Œnothera was given before the Zoological Seminar of Columbia University, April 23, 1903. The comparisons between the mutants were not completed until August, 1903.

gations have, or should have, their chief purpose in the discovery of the physical mechanism of heredity.

The terms *discontinuous variation*, or *mutation* in connection with the study of inheritance, descent, and the origin of species may be taken to mean the autonomous physiological processes by which one or more individuals of a species give rise to offspring which exhibit qualities, or groupings of qualities not possessed by their immediate ancestors and not previously exhibited by the individuals comprised in the parent species (progressive mutation), or by which one or more individuals give rise to individuals lacking qualities or groupings of qualities exhibited by the ancestral forms (retrogressive and degressive mutation). These aberrant individuals or mutants may transmit their characters to their offspring in such a manner as to give rise to a new line of descent constituting the origin of a new type by mutation.

The number of freaks, sports, bud-variations, and specimens of plants with abnormal forms and sizes of leaves, stems, and flowers, some of them highly teratological, to which attention has been called by various writers in botanical periodicals under the designation of mutants makes necessary the emphasis of the fact that observations on a single individual, or a single generation of individuals are of but little value in distinguishing fluctuating variations from mutations. Results worth a moment's consideration may be obtained only by the most careful exclusion of the possible effects of disease, of animal or plant parasites, of hybridization, and by a careful analysis of the phylogenetic value of the divergences as tested by observations on successive generations of living forms. It is in this manner, and in this manner alone, that discontinuous, saltatory variations may be distinguished from the results of common, fluctuating and individual variability. Mutation rests in the main upon such substantive, discontinuous variations as the acquisition of new characters, or the loss of old ones hitherto transmitted by the parent type, or upon simultaneous alterations of both kinds. These changes may be accompanied by, or may result in, the masking of current qualities, or the unmasking and energizing of latent qualities of the parent type.

The essential differences between the two processes appear to have been originally set forth by Charles Darwin,[1] and are treated at length by deVries. The formal distinctions drawn by deVries appear to need some slight modification and elaboration in order to make them universally applicable. Thus he holds that continuous, or fluctuating variability occurs only in accordance with Quetelet's laws, and that it involves only the number, size and weight of organs, and does not include differences in qualities. Cultural experiments of various kinds during the last few years have given results in which the qualities as well as the number, size and structure of organs have been materially altered, but such induced variations or divergences were not transmissible. This particular factor in distinguishing between fluctuating and mutating variability therefore becomes a safe one, when it is modified to make mutating variability include only newly acquired and transmissible qualities. The presence of a plant or an animal parasite may not only change the mechanical features of an organ but may also cause most radical alterations in its physiological properties. A single example of the latter may be cited in the case of the common species of Euphorbia in which the affected leaves alter their geotropic sensibility in such manner that they change from diageotropism to apogeotropism. Such variations are not transmissible however, and in this lies the true test between mutation and fluctuating variation. A still further distinction consists in the fact that mutations ensue in the rudimentary state of the individual, while the alterations in qualities induced by any of the above factors in fluctuating variability may be caused in various stages of the development of the individual, but in a rudimentary stage of the organs concerned. Mutative alterations arise with the individual, are not the direct result of external factors, and are perfectly transmissible, while fluctuating variations may arise by the influence of external factors at various stages in the individual development, and are not transmissible in their entirety.

Much of the confusion inevitable to any discussion of the subject may be avoided if it is borne in mind that we habitually

[1] DeVries. *Mutationstheorie*, Bd., 2, 1903.

deal with two different conceptions under the term species, one based upon systematic and the other upon physiological, or sexual affinities. The last named conception considers species as phylogenetic groups embodying certain elementary characters and showing certain capacities and habits, some of which may not find expression in external form and structure. The systematic conception of species runs closely parallel to the above and should finally express the actual blood relationship of all of the forms in the vegetable kingdom. It is practically impossible however, to take into account features not actually expressed in some definite measurable structure, or which may not be determined by some rigid physical standard, and comply with taxonomic methods. Thus numerous undoubted instances are known of two or more groups of forms embodying separate lines of descent, which, however, may not be separable by taxonomic standards. The present discussion is of course concerned only with the physiological conception of species, although as may be seen by an examination of the features of the mutant forms brought under consideration, these present anatomical characteristics sufficient to warrant their recognition upon any taxonomic basis.

The special purpose of the present paper is to consider discontinuous variation as a probable method of the origin of new species, and to present the results of two season's observations on the form, habit and behavior of some of the mutant forms discovered by deVries seventeen years ago.

The observation and recording of marked examples of discontinuous variation in lines of descent is as old as biological science itself. Recently this procedure has been brought into the focus of attention anew as the result of the deVries investigations, which tend to demonstrate that it is an important means by which species come into existence. More than three centuries ago (1690), Sprenger the apothecary of Heidelberg, who had *Chelidonium majus* under cultivation, noted the sudden appearance of a type with laciniate leaves in his garden. This form which is also distinguished by other characteristics, was found to be constant and self-maintenant in competition with the parent type, and has remained distinct to the present day with-

out artificial selection, and no specimens have ever been seen which could not be traced back to this original lot of individuals in Heidelberg. The citation of a large number of equally well or better authenticated instances of the sudden origin of types is to be found in Korschinsky's memoir to which reference is made below.

The space at command does not permit even an outline of an historical sketch of the views of the more prominent writers on descent, concerning discontinuous variation as a means of origin of species. It may be said, however, that Darwin attributed some importance to "single variations" in his earlier writings but seemed to relinquish this favorable view of the matter under the pressure of criticism to which he was subjected in connection with all phases of his opinions on the origin of species. Kölliker's theory as to the transmutability of egg elements as a means of heterogenesis in 1864 will be recalled in this connection.

Dollo is credited by deVries with being the first to announce definitely the conclusion that species might originate by mutation (1893) (*Mutationstheorie*, Bd. 1 : p. 46). Bateson goes so far as to say in his summary of *The Material for the Study of Discontinuous Variation* (1894) that "It (The evidence of variation) suggests in brief *that the discontinuity of species results from the discontinuity of variation.*

Korschinsky (1899) published a most valuable historical account of the better authenticated instances of types supposedly originating by discontinuous variation, and made a comparison of the theories of natural selection and heterogenesis. The German reprint of his paper (*Flora*, 89, pp. 240–363, 1901) is the completest yet published in citation of facts and in review of pertinent literature, and it forms a logical historical prelude to the observations of deVries.

The first well-guarded scientific observations of the origin of new types as a result of discontinuous variation were made by deVries, who by the expenditure of a great amount of labor carried out an extensive series of experiments in the cultivation of plants of the old *Œnothera lamarckiana* type. The general facts obtained by him have been brought to notice repeatedly

within the last three years and it will not be profitable to rehearse the details at this time. Briefly stated deVries's investigations may be embodied in the following paragraphs.

1. Observations were chiefly concerned with a large number of plants growing wild and under cultivation, of the type of *Œnothera lamarckiana*. The identity of the parent form was found by comparison with the original description of the plant made a century earlier, and by comparison with a type specimen in the Muséum d'Histoire Naturelle in Paris collected in 1788. The actual name of this plant in the revised nomenclature is a matter of minor importance in the present connection.

2. Numbers of individuals of the parent type, as a result of cross- and self-pollination indifferently, constructed seeds which developed into independent forms, constant and self-maintenant, which differed in habit, structure, stature, appearance and properties from the parent type.

3. The aberrant or mutant forms might be divided by characters as sharp and numerous as most of the so-called minor species of the systematist.

4. No forms intermediate between the mutants, or between the mutants and the parent type were found.

5. That the mutant forms were really groups of phylogenetic value was proven by their behavior when crossed with one another, with the parent form, and with other species in the same genus. The hybridization experiments with these forms has yielded some exact evidence as to the preponderance of phylogenetically older characters by reason of the fact that the mutants are forms the exact ages of which are known. Of the crosses of *Œ. lata* and *Œ. nanella* with the parent form, from a half to three-fourths were found to be of the parent type, and the remainder of the mutant type form. The crossing of mutants with each other produces a generation many of which show reversionary characters. The mutation hybrids are constant in succeeding generations. The separation of antagonistic characters in the first generations is weighty evidence in support of the theory of elementary characters, and for the mutation theory.

6. The new types were either constant from the beginning, or if weak, inconstant or perishing, showed no tendency to revert

to the parent type, and their constancy or fixity might not be increased by artificial selection.

7. More than one mutant might arise simultaneously from the parent individuals.

8. Any one of the several mutants observed might originate from several parent individuals simultaneously.

9. The mutant forms might arise from successive generations of the parent types.

10. The mutant forms might in turn give rise to new types after their separation from the parent type.

The above statements rest directly upon observations of carefully conducted experimental cultures and admit of but little argument as to interpretation. With this positive evidence at hand questions at once arise as to the frequency, occurrence, prevalence, exclusiveness, and as to the mechanism of discontinuous variation as a method of origin of new species. When we take up these points we at once enter a field of speculation in which it may be seen there is opportunity for unlimited argument, and in which with the bias to which most of us are subject as a result of our training and investigations, it is difficult to maintain a purely judicial attitude. It will be profitable to recall some of the more important facts bearing upon these matters however.

First, as to the occurrence of discontinuous variations in plants the following examples cited by Korschinsky will be illustrative: *Erythrina crista galli* was introduced into cultivation in 1771 and no aberrant forms were seen until seventy-three years later: *Begonia semperflorens* showed deviating forms only after fifty years: *Cyclamen persicum* gave no unusual forms until after one hundred and twenty years of observation: no mutations were observed in *Ipomoea purpurea* in one hundred and twenty years.

De Vries observed many thousands of individuals of a hundred species growing in the vicinity of Amsterdam in 1886 and 1887 and found mutations in only one, that one *Œnothera lamarckiana*. He points out that remains of plants of various species found in mummy cases four thousand years old have been found identical with living species in all recognizable characters. As a result of a rough examination he also concludes that the

elementary characters of any species of a higher plant may be reckoned at a few thousand — about 6000 in Œnothera. If Lord Kelvin's estimate of the period during which life has existed on the earth is accepted it might be concluded that in a general way the average interval separating mutable periods of any plant must be several thousand years, although nothing in the nature of the question may be taken to indicate anything like uniformity in the matter. Some writers have put forward the conclusion that at least ten times the above named period, or twenty-five hundred million years, would be necessary for the derivation of the existing forms of plants and animals by natural selection. It must be admitted that both ideas are valuable chiefly as attractive examples of imaginative grasp rather than as affording any real evidence in the matter.

It will be recalled that the various theories which have been put forward to account for the origin of species have been held by their authors and advocates to be mutually exclusive, and it seems to have been, and is still taken for granted by the majority of writers, that all organic forms, both plants and animals, have arisen in the main by one simple method of biological procedure. The development of biological science has certainly reached a stage where this a priori generalization may well be abandoned. I can not say that a candid review of the mechanism of protoplasm, or of the pertinent evidence, from any point of view compels adherence to this ancient assumption.

The great amount of critical study that is being directed to the study of hybrids and hybridization is widening the horizon of this subject momentarily, and the result of our recently acquired information leads us to conclude that species may originate by crossing. In such instances the new types are due either to new combinations of unit characters or to reversionary qualities, it being necessary to keep in mind the fact that by such union of two types no new characters are brought into existence. It must be regarded as unsafe moreover to declare any plant a hybrid of any other given forms unless the process of origin has been carefully followed. The fact remains that hybridization is a demonstrated source of origin of species however, and it is becoming more and more generally recognized that more than one method

of procedure may have been followed in the development of the prevalent types of vegetal organism. This view of the subject has been thoroughly discussed by von Wettstein and need not occupy our attention further at the present time (*Bericht, deut. Bot. Gesell.*, Bd. 13, p. 303, 1895).

DeVries concedes that species might originate by more than one method, but he holds that natural selection may account for neither the origin, nor the preservation and continuance of species. He furthermore calls attention to the fact that Darwin repeatedly asserted that characteristics or qualities were formed very slowly but might disappear suddenly, or in other words that retrogressive and digressive species formation might ensue by discontinuous variation or mutation. (*Mutationstheorie.* Bd. 2: 661. 1903.)

It is necessary to point out that the use of the term *natural selection* as applying in any sense to the *origin* of species by mutation is wrong in view of the special meaning long attached to that phrase. Natural selection implies constant and progressive variation in one or many directions, the individuals distinguished by the greatest improvements constituting the fittest and surviving from successive generations. The constant and repeated survival of the fittest and most improved effecting in time such an amount of departure from the original as to constitute a new type. The mutants which arise in discontinuous variability are seen to depart in all directions from the original, but none of these may be fitter than the parent type and may perish. It is probable that many thousands of mutants come into existence for every one that is capable of existence in competition with the parent type. The repeated failure of the successive series of mutants can in nowise affect the character of the later crops of discontinuous derivatives, and hence the failure of the non-fit and the endurance of the improved form are not dependent upon natural selection. Every mutant that survives must not only be suitable for its environment but must be of a structure and habit that will enable it to compete successfully with existing types, in comparison with which it is enormously weaker in numerical strength. It must therefore gain a foothold at once, with but little opportunity for adaptations of any kind. Every mutant is

a possible species and the only selection which might be said to act is that which determines the type able to live: this selection has nothing to do with the origin of the surviving form however.

Thus of the sixteen mutants discovered by DeVries one had already established itself when found, although seen to arise anew from the parent type subsequently. Perhaps one or two of the others might have succeeded in gaining a foothold, but the majority of the new forms must have inevitably perished if subjected to the ordinary competition of the prevailing meadow species.

As to the cause of mutation, and the mechanism of the process but little except of a speculative nature may be offered. Korschinsky assumes that heredity and variability are opposing forces or tendencies which are ordinarily balanced. External agencies such as successive seasons of good nutrition might allow the tendency to variation to overcome the hereditary stability and allow the origination of a new form as a result of the unloosed, superfluous unbalanced energy. He supposes that whatever the agencies may be that cooperate to bring about the mutative condition, these forces act upon the developing embryo in the seed, although he hazards no guess at the manner in which this might be accomplished (*Flora*, 89: 240, 1901). The above it may be noted is in direct contrast with the proposal of Darwin that the development of new types is more rapid when species are competing under adverse conditions, or when the struggle for existence is fiercest.

So far as DeVries's theory of mutation is concerned it may be said to be the logical outcome of, and to rest upon his hypothesis of intracellular pangenesis. By this, protoplasm is taken to consist of ideally minute pangens, which make up the living substance. The pangens and aggregations of pangens are the bearers of the elementary characters of the species. Alterations in the numerical relations of pangens are made to account for fluctuating variability. The inactivity of pangens and groups of these units would cause degressive or retrogressive mutation. The formation of new characters in progressive mutations would depend upon the development of new pangens, this process constituting premutation. The formation of identical pangens in separate species would account for parallel mutations.

But little definite evidence is at hand as to the time at which the changes antecedent to mutation, constituting pre-mutation occur, although certain stages of development may be designated, previously to which they must come about. Mutations of the higher plants are first apparent in the seedling but the actual alterations or departure from the hereditary behavior must have taken place at least as far back as the formation of the sexual elements the union of which produced the embryo, and may have occurred even earlier. In any case the mutants are perfectly formed in the embryo and influence of any kind upon the germinating seed may not alter their nature (see page 746). It may be seen from the foregoing that the mutative processes may be connected with either the vegetative body or the sexual elements, and may be found within the sporophyte, or be confined to the gametophyte.

If the pre-mutative alterations occur in the vegetative protoplasts of a self-fertilized individual both gametes would presumably carry the same characters to the union. If, on the other hand, premutation occur in one of the sexual elements, or if it occur in the vegetative cells of species which are cross fertilized only, the embryos formed would be the result of the union of one mutant gamete and one of the regular inherited form. In a sense such mutants might be considered as hybrids. This theoretical aspect of the question seems to find a reflection in the behavior of *Œ. lata*, one of the mutants with pistillate flowers only. When pollinated by the parent form, *Œ. lamarckiana*, it produces *Œ. lata* and *Œ. lamarckiana*.

DeVries conjectures that the causes inducing mutation are partly internal, and partly external to the organism. The state of external factors necessary to the process probably occur only at uncertain intervals, and is supposed to embrace a combination of extremely favorable and unfavorable conditions.

Probably no more profitable subject for research in the whole realm of natural history offers itself to the investigator than the problem of the causes which produce new species. The above supposition deserves early attention from the experimentalist since it is one that is comparatively easily capable of proof and disproof.

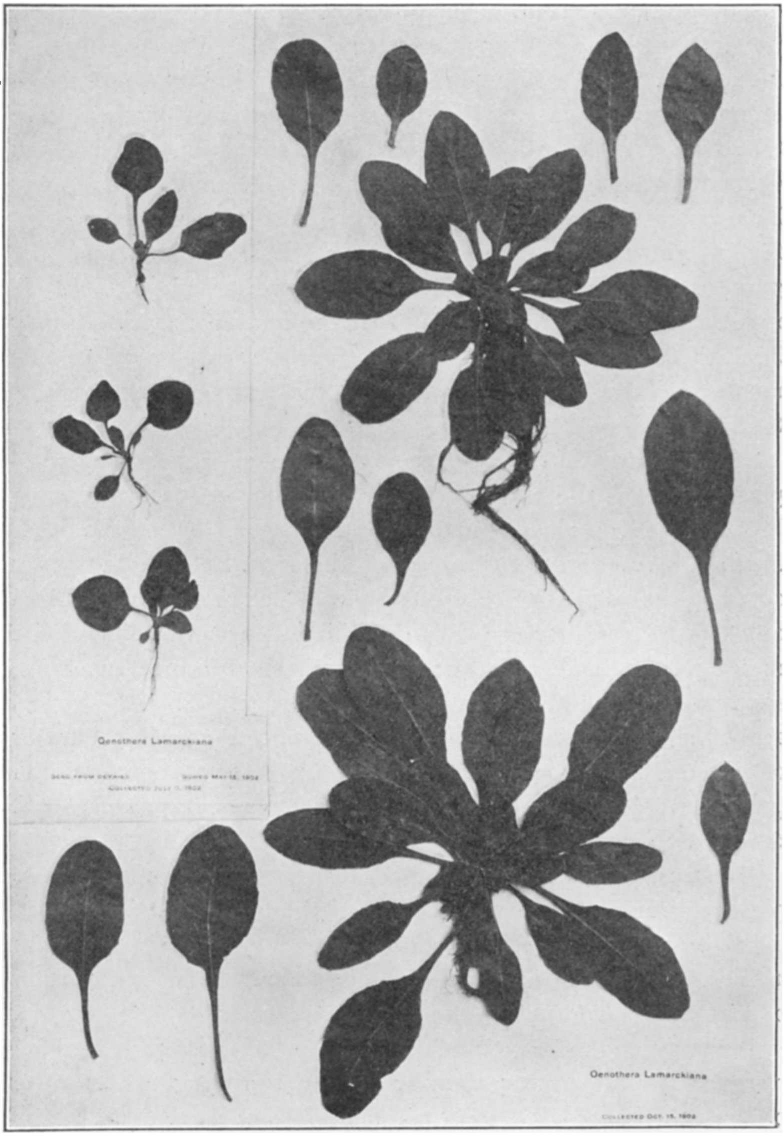

Fig. 1.—*Œnothera lamarckiana.* Rosettes of seedlings two months, and five months of age. Photographed from herbarium sheets. (See Figs. 2 and 3.)

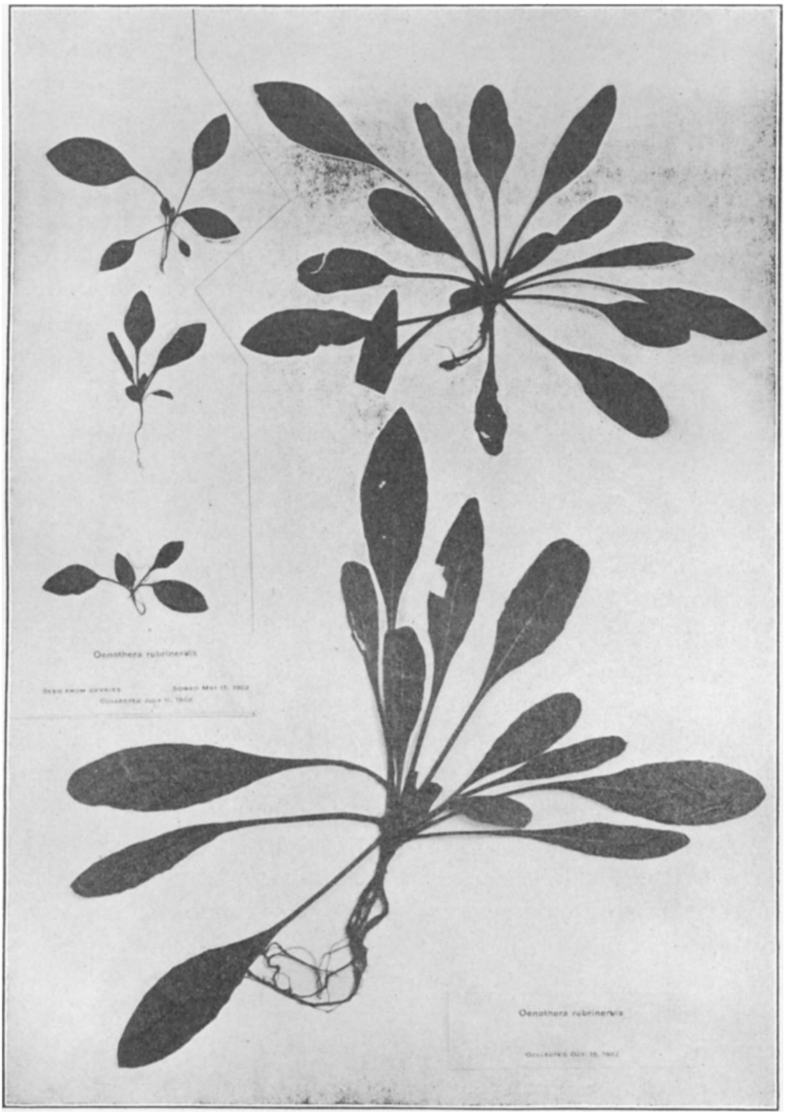

FIG. 2. *Œnothera rubrinervis.* Seedlings two months, and five months of age. Photographed from herbarium sheets. (See Figs. 1 and 3.)

Being desirous of testing the general facts of mutation as illustrated by the behavior of the œnotheras under environmental conditions different from those at Amsterdam, seeds of *Œ. lamarckiana*, *Œ. rubrinervis*, *Œ. lata*, *Œ. nanella*, *Œ. brevistylis*, and *Œ. gigas* were procured from Professor DeVries and these were placed in soil in the propagating houses of the New York Botanical Garden May 15th, 1902. Germination followed in a few days, and a number of individuals ranging from fifteen to forty of every species were pricked out and suitably repotted from time to time. The cultures were examined three to seven times per week except during February, 1902, and July, 1903. The amount of work necessary to make minute and exact observations on all of the above forms being too great a demand upon my time, chief attention was devoted to a comparison of the parent type with *rubrinervis* and *nanella*, two mutant forms.

In order to systematize the results general notes were made continuously upon the habits of the growing plants and formal comparisons were made at successive stages as follows:

First stage.— July 11th, 1902. The plantlets were nearly two months old and still retained the cotyledons.

Second stage.— October 15th, 1902. A distinct tap root had been formed and a rosette of leaves had been developed.

Third stage.— June 1st – 10th, 1903. Adult rosettes had been formed, and the smaller leaves which appear around the base of the stems were apparent. Some flowering stems were beginning to push up.

Fourth stage.— August 10th–15th, 1903. A number of inflorescences had been produced and flowers were opening daily in great profusion on some of the forms. Some of the inflorescences were enclosed in paper bags in order to secure pure seeds by means of artificial transfer of pollen.

The more apparent anatomical differences among the forms examined are shown quite strikingly by the series of photographs and drawings which illustrate this article.

The main fact to be kept in mind in regard to the parent form is that it is a recognized and constant species, which has not undergone noticeable alteration during the long period it has been under exact observation. The seeds from which the

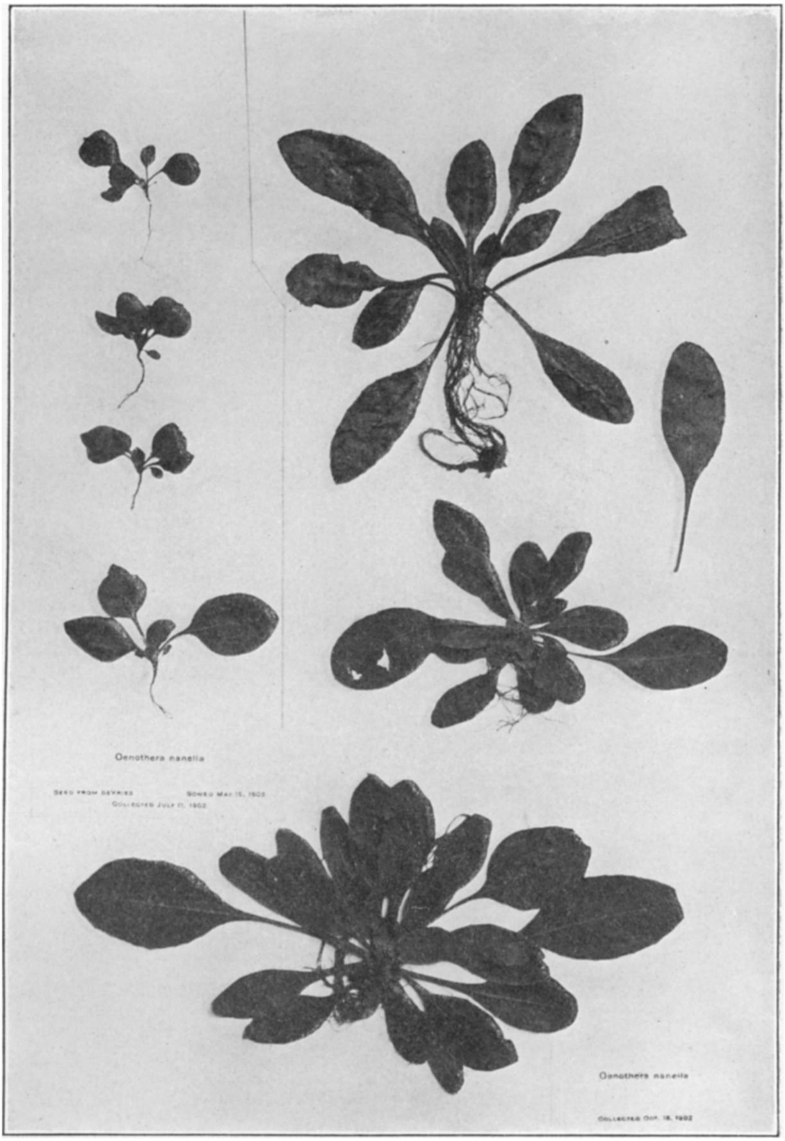

FIG. 3 —*Œnothera nanella*. Rosettes of seedlings two months, and five months of age. Photographed from herbarium sheets. (See Figs. 1 and 2.)

experimental material was derived were sown in a bed at s' Graveland near Amsterdam in 1875 and had been allowed to spread over an adjoining neglected field until in 1884 an area of 2800 square meters was covered. This material showed the presence of a form so different from the parent type, when examined by deVries in 1886, as to lead him to consider it as a new species, and this mutant, *Œ. brevistylis*, which did not arise again during the observations, maintained itself in the same locality during a period of twelve years, records of it having been made as late as 1898, and it is still cultivated among the other mutants grown by deVries and myself. Other forms appeared during the course of the next fourteen years as has been described in detail.

It was deemed advisable to make independent comparisons of the plants grown in my own cultures with the type specimen with which deVries identified his parent form, and to this end Miss A. M. Vail made a visit to the herbarium of the Muséum d' Histoire Naturelle in Paris, in May, 1903, at my request, and also later a journey to Amsterdam and inspected the cultures of *Œnothera* under Professor deVries's own guidance. Miss Vail has kindly prepared the following report on the matter:

"The parent form, *Œnothera lamarckiana* Ser. was found by deVries to agree in every particular with two specimens in the Muséum d'Histoire Naturelle in Paris. These specimens consist of, first: a plant cultivated in the Paris Garden that had formed the basis of the original description of *Œnothera grandiflora* Lam. It bears a label indicating it as having been included in the herbarium of Lamarck which was acquired by the Museum in 1850. On the margin of the sheet in the handwriting of Poiret (the author of the section dealing with *Œnothera* in Lamarck's Encyclopedia) is the following inscription 'Œnothera—(grandiflora)—nova spec. flores magni lutei, odore grato, caulis 3 pedalis.' This specimen is in flower only and consists merely of the branched upper portion of the shoot with numerous rather small leaves and conspicuously large typical flowers. The second specimen comes from the cöllection of Abbé Pourret that was contained in the collections of Dr.

[1] For a brief general account of the experimental cultures, see MacDougal, The Original of Species by Mutation. *Torreya*, Vol. 2, pp. 65–68, 81–84, 97–100, 1902.

Barbier inherited by the Museum in 1847. It is filed in a cover with *Œ. biennis* L., and bears that name on the sheet, a small label inscribed with a series of prelinnean names, and another with '*Onagra vulgaris* Spach' and '*Œnothera biennis* Linné,' both apparently in Spach's handwriting. This is the plant referred to by de Vries as having been collected presumably by Abbé Pourret in the Paris Garden during his visit in 1788. The specimen represents an unbranched upper portion of a shoot with numerous large well-developed leaves, partly mature capsules and several flowers that are somewhat smaller than those of the previously mentioned specimen. These two specimens differ in no important particular. Tracings of them compared with living plants grown in the New York Botanical Garden from seeds sent by de Vries agree quite perfectly.

"A search through the herbarium of the Muséum d'Histoire Naturelle and that of the New York Botanical Garden does not bring to light any specimen of a wild North American plant that can be referred to *Œ. lamarckiana* as it is now known and cultivated in Europe, nor does it seem to be known to collectors in North America at the present day.

"Several specimens were found however, which might be conjectured as representing a North American plant from which *Œ. lamarckiana* might have been derived. One of them is a plant collected by Michaux now preserved in the Muséum at Paris, and cited by de Vries in the Mutationsteorie (Bd. 1 : p. 316) and referred by him to a plant frequently cultivated in Europe under the name of *Œnothera grandiflora* Ait *Œ. suaveolens* Desf. but which he considers different from *Œ. lamarckiana.* A tracing was also made of this plant which consists of two specimens fastened on the same sheet upon which numerous inscriptions bear witness to much diversity of opinion as to its real identity. A small slip of paper bears in Michaux's handwriting '*Œnothera grandiflora*,' another (the customary label of the Michauxian specimens) the inscription '*Œnothera grandiflora* Poiret Encycl.,' in the writing of that author of the section dealing with *Œnothera* in Lamarck's Encyclopedia; beneath that '*Œnothera suaveolens* Hort. par.' in the writing of Desfontaines, and lastly '*Onagra vulgaris grandiflora* Spach.'

in the writing of Spach. The larger of the two specimens consists of a simple entire plant not fully developed, showing root, leaves, flowers, and capsules, but no basal leaves. The other specimen, which is smaller, is incomplete and fragmentary. A comparison of the tracing of the larger specimen with material in the herbarium of the New York Botanical Garden shows that it is identical with a specimen under the name of *Onagra biennis grandiflora* (Ait) Lindl., collected by E. S. and Mrs. Steel on Stony Man Mountain, Luray, Virginia, August 15th, 1901. The comparison also shows that the wild plant has undergone no change of any kind during a period of over a century.

"The following memoranda and citations may be of interest as throwing some light on the history of *Œ. lamarckiana* previous to 1788.

Linnæus in his Species Plantarum says that *Œnothera biennis* was brought from Virginia in 1614 and was then (1753) common in Europe. In Hortus Cliffortianus (1737) he states on p. 144, that it is a native of Virginia, having been brought from there to Europe 120 years before and was at the time he wrote spontaneous and plentiful in the fields of Holland. In Hortus Upsaliensis (p. 94. 1748) he gives the date of its introduction as 1620, then declared it to be spontaneous in Belgium, Italy, 'Gallia and Germania.' So that from the middle of the 17th century it was generally in cultivation in the botanical and horticultural establishments of Europe.

Referring to some of the prelinnean writers we find that Tournefort in *Inst. rei. herb.*, on p. 302 (1700) enumerates nine species of Onagra, the first four of which only are of interest here, as follows:

(1.) *Onagra latifolia. Lysimachia lutea, corniculata.* C. B. Pin. 245.

(2.) *Onagra latifolia, flore dilutiore. Lysimachia corniculata non papposa, Virginiana, major, flore sulphureo.* H. L. Bat.

(3.) *Onagra latifolia, floribus ampliis. Lysimachia Virginiana, altera, foliis latioribus, floribus luteis, majoribus. Cat. Altdorf.*

(4.) *Onagra angustifolia. Lysimachia angustifolia, Canadensis, corniculata* H. R. Par. *Lysimachia corniculata, lutea, Canadensis minor, seu angustifolia* Mor. H. R. Bles.

In the first of these references Caspar Bauhin in *Pinax* on p. 245 (1671) writes of an American evening primrose under the name of *Lysimachia lutea corniculata*, as being a Virginian Lysimachia growing in the Garden at Padua in 1619 and adds that it was a pleasing plant and easy to propagate from seed. The second reference goes back to Hermann's Catalogus, 1687, where on p. 396 he records a species of Virginian *Lysimachia* with sulphur colored flowers as growing in the Garden at Leyden. The third reference is to a plant with larger leaves and larger flowers from the Altdorf Garden. In Jungermann's *Catalogus plantarum quae in horto Medico Altdorphino reperiuntur* we read that a *Lysimachia lutea Fl. majoribus, odore Tabaci.* and a (Lysimachia) *Virginiana lutea Delphinium quorundum*, were known in the old Bavarian garden at Altdorf in 1635 and the statement is again repeated in another *Catalogus* in 1640. It was a sufficiently remarkable plant for Tournefort to note especially in his Institutiones, and it might be inferred that this large flowered plant from Altdorf was the ancestor of *Œnothera lamarckiana*. It would appear as if a form of what is generally claimed to be *Œnothera biennis* L. with delicate sulphureous flowers grew in the Leyden Garden and another with larger flowers in the garden at Altdorf. Under the same name, *Lysimachia corniculata*, an American evening primrose is said to have been growing in the Messina Garden in 1640 and it was known in the Paris Garden at about the same time or a little earlier and in 1653 in the Copenhagen Garden. Morison also records it as occurring in the Hortus Blesensis in 1669. This last reference is the one quoted by Tournefort as his fourth species. Again under the same name of *L. corniculata* Sherard speaks of it on p. 44 of his Schola Botanica as growing in the Paris Garden in 1689 and, presumably, descendents of the plants he saw were those collected by Abbé Pourret a century or so after and later made the type of the much discussed *Œ. grandiflora* Lem. = *Œ. lamarckiana* Sen. The plant described by Linnæus in the Species Plantarum was doubtless a composite species and it would be particularly interesting in this connection to know just what he meant by the plant described in the *Hortus Cliffortianus* as being plentiful in the fields of Holland. A tracing of the speci-

men which could be considered as the type of the plant described by him in the Hortus Cliffortianus has been kindly furnished by Dr. A. B. Rendle of the British Museum, and although the flowers are somewhat smaller than those of the living plants of *Œ. lamarckiana* as grown in the New York Botanical Garden nurseries, yet the general characters are identical, notably that of the entire or slightly emarginate petals. This character is certainly not typical of the wild weed-like *Œ. biennis* of waste lands

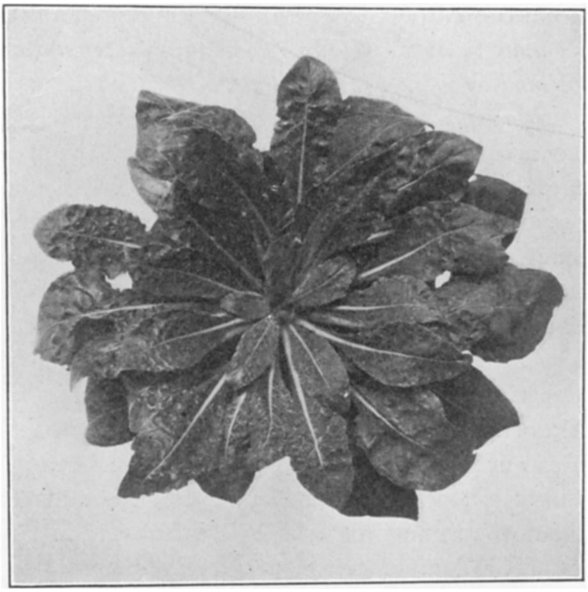

FIG. 4.—*Œnothera lamarckiana*. Adult rosette immediately preceding development of flowering stem. Photograph of living plant taken from directly above. (See Figs. 5 and 6.)

in North America to-day. In any case it seems extremely doubtful that all these cultivated evening primroses should be referred to so ungainly and unornamental a plant as *Œ. biennis*.

Prof. deVries in an article on the introduction of *Œ. lamarckiana* in Holland (Ned Kruidk. Arch. ser. 2, Vol. 6, p. 579, 1895) gives a long and detailed history of the ancestors of the plants taken into cultivation for his experiments. They were traced to plants escaped from cultivation and originally raised from seed received from a seedsman of Erfurt, Germany. Prof.

deVries also states that *Œ. biennis* and *Œ. muricata* are found in Holland, notably on the dunes.

It seems well established that a large flowered Œnothera was seen in the Altdorf Garden in 1635, which is probably referable to none other than *lamarckiana*. Later notes of its occurrence are in existence, but the first definite record of the species was

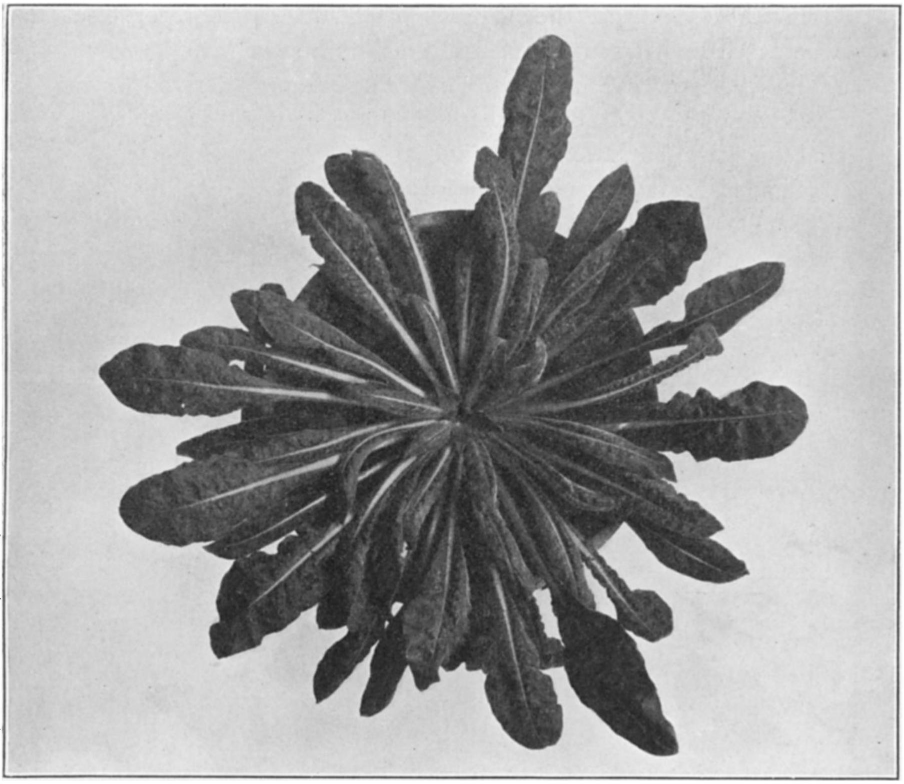

FIG. 5.—*Œnothera rubrinervis*. Adult rosette immediately preceding the development of the flowering stem. Photograph of living plant taken from directly above. (See Figs. 4 and 6.)

in 1788. It has been found constant since this date, both in gardens and when running wild: its evolutionary procedure is therefore none the less valuable as scientific evidence than as if it were an indigenous wild growing species.

Œnothera lamarckiana is a species which, so far as present

knowledge is concerned, has no exact duplicate in the native flora of any region, and two probabilities are suggested as to its origin: It may have been a native of a restricted range in "Virginia" in which it has been exterminated by agricultural operations, and hence cannot be found at the present time: or it may have arisen by some such sudden, and abrupt, discontinous variation, as that by which deVries' mutants came into existence, from *Œ. biennis* in the gardens, at Padua, Altdorf or elsewhere: at least no intermediate forms are known."

Only eleven specimens of hybrid seedlings derived from *Œnothera lata* were brought to the adult stage, in my cultures and of these but two conformed to the type of *Œ. lata*, the remainder being the *O. lamarckiana* form. *Œ. lata* does not perfect its stamens but it is capable of being pollinated from the parent. The offspring followed the laws governing parent and mutant hybrids, which with deVries were found to consist of 18% to 20% of the mutant type and the remainder of the parent. My own results agree with this. It is clear that this form would not have survived beyond the season of its appearance as it does not display any marked propagative capacity.

Œnothera nanella originated in deVries's cultures in 1888 and has since been followed by him through fifteen seasons. The qualities of this form separate it from the parent in such manner that it might be considered as a variety by some systematists, although its behavior and physiological properties are constant and very clearly distinguishable. In following out the development of the plant during the eighteen months over which my own observations extended it became evident that it differs most widely from the parent in its earlier, and also in its adult stages, being most like it in the full rosette stage. The most apparent feature is its diminutive size, both in the young plant and in the mature flowering shoot. The stem shows but little capacity for branching and did not reach a height of more than 20 to 25 cm. in my cultures, or about one fourth that of the parent, which sends out numerous vigorous branches. The first few leaves have very broad laminæ with irregular apical portions, and are short petioled. Later leaves are more nearly like the parent type but remain shorter petioled which has the effect of

making a denser more crowded rosette. The bases of the lamina are almost cordate in some instances, and vary from oblong ovate to ovate in outline, being sparingly toothed. The plants established in the soil in the open air did not bloom until about three weeks later than the parent and *Œ. rubrinervis.* No noticeable departure from the characteristics assigned this form by deVries was found.

Seedlings of *Œnothera rubrinervis* were seen to have narrower leaves throughout from the earliest stages. The rosettes were very closely appressed to the soil, and in this stage the margins of the long petiolate leaves were inrolled, thus decreas-

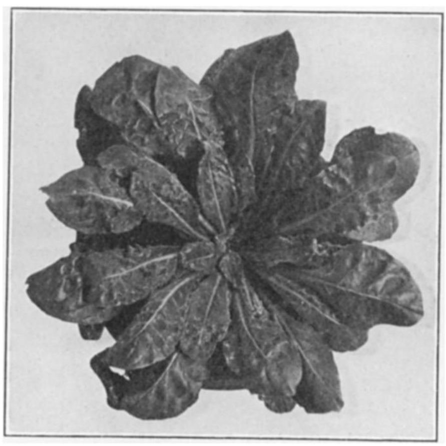

FIG. 6.—*Œnothera nanella.* Adult rosette immediately preceding the formation of flowering stem. Photograph of living plant taken from directly above. (See Figs. 4 and 5.)

ing their apparent width. Attention is to be called here to the fact that comparisons of leaf forms in plants of this kind are permissible only between organs on corresponding portions of shoots. The laminæ were more bluntly toothed than those of the parent type, and the midribs occasionally bore a tinge of red, while the entire shoot including the leaves of the upper part of the stem showed a tendency to the formation of anthocyan. The physical qualities of the leaf were strikingly different from those of the parent, perhaps the most noticeable feature being the great brittleness of the leaves and stems of

young plants, indicative of high turgidity and weak development of mechanical and supporting tissues. Both of these characters have been observed by deVries, who notes that the bundles of

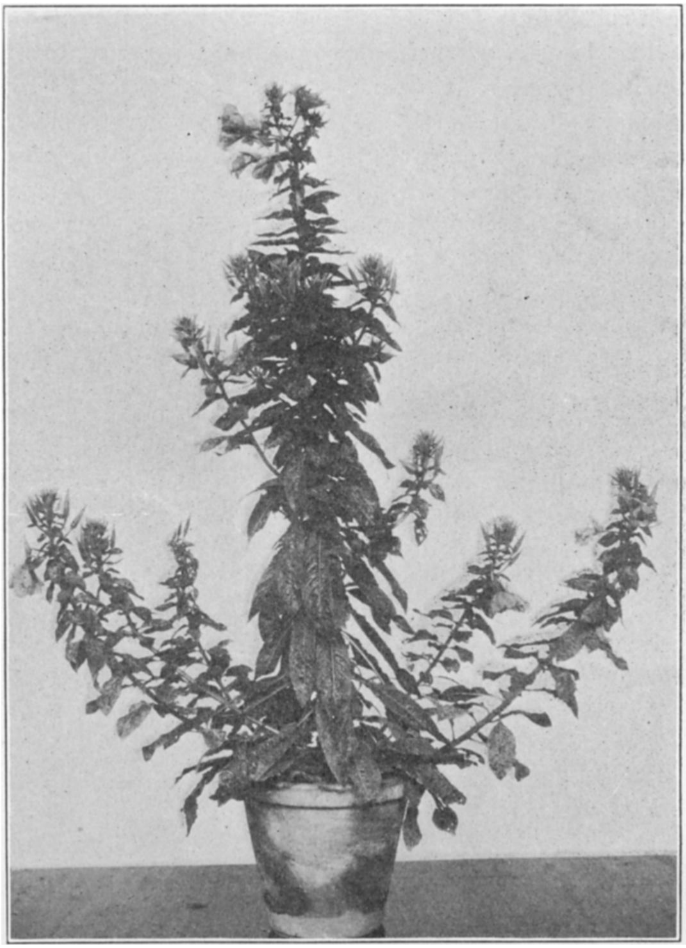

FIG. 7.—*Œnothera lamarckiana.* Adult plant two weeks after beginning of opening of flowers. Photograph of living plant grown in the soil in the open air, and temporarily fixed in a pot. (See Fig. 8.)

bast fibers of the flowering stems were composed of elements with thinner walls than those of the parent type.

The leaves of the full rosettes, were silvery white owing to

the fact that the hairs on both surfaces were both longer and more numerous than on the parent type. The average length of the hairs on the upper surfaces was 35 as compared to 28 in the parent type, and on the lower surfaces 42 as compared to 30. The average number of stomata on a unit of area of the upper surface of the leaves of *rubrinervis* was 37 as compared

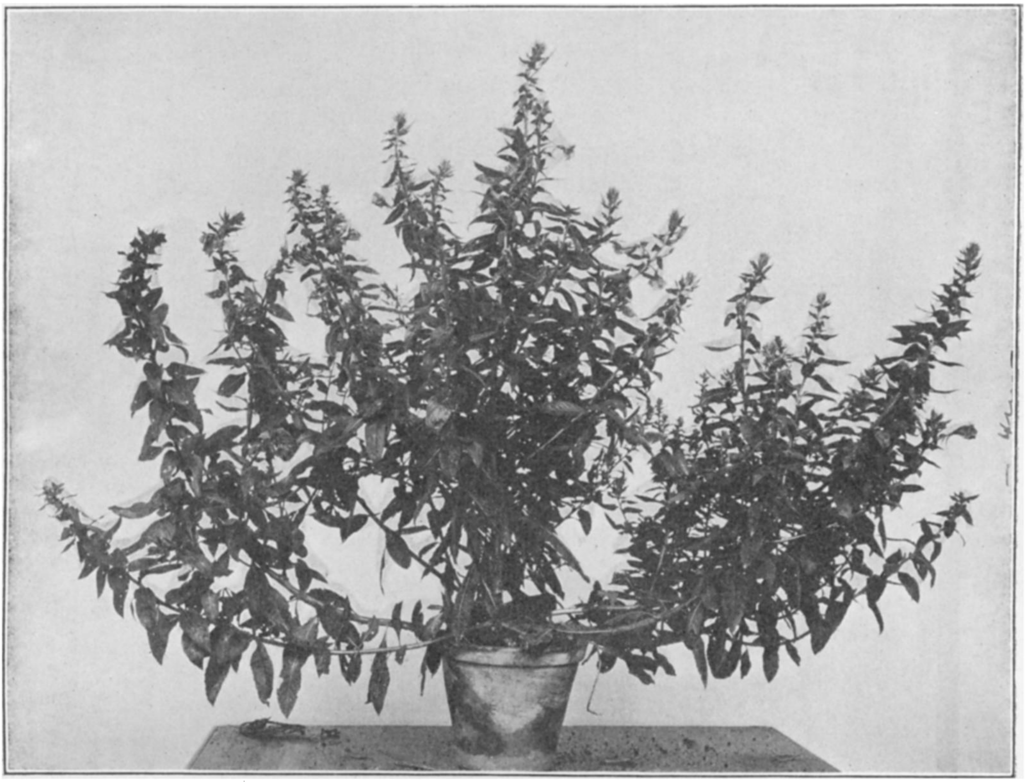

FIG. 8.—*Œnothera rubrinervis*. Adult plant two weeks after beginning of opening of flowers. Photograph of living plant grown in the soil in the open air, and temporarily fixed in a pot. (See Fig. 7.)

with 34 in *Œnothera lamarckiana*. The brittleness characteristic of the tissues of *rubrinervis* may be seen to extend even to the hairs, since these structures are easily detachable from the dried specimens, and hence giving rise to the conclusion that *rubrinervis* is less densely pubescent than *lamarckiana* as given in the systematic description below.

Still another major difference between the forms in general habit is that of the method of branching and the growth of the branches. In *Œ. lamarckiana*, the branches from the basal portion of the shoot were of a length amounting to more than half that of the shoot which is also true of *Œ. rubrinervis*. The upper branches of the former remain short and stout however, while those of *rubrinervis* attain greater lengths which decrease upwardly so that a plant may have a roughly globular outline.

The majority of the features in which the mutant departs from the parent, as described above, are of a nature that would equip the new form for living under more arid conditions than the parent, although the actual endurance of *rubrinervis* to decreased supply of moisture was not tested. So far as this single observation goes then, it is to be seen that the new characters of mutants are harmonious in their adaptive relations.

Œnothera rubrinervis originated in deVries' cultures in 1899, and has also appeared by independent mutations since that time. It has been found to be independent and self-maintenant in competition with the parent form.

A large number of flower buds in both *rubrinervis* and *lamarckiana* were pierced by some insect, and the larvæ coming from the eggs deposited made great destruction, and also caused the abnormal enlargement of the buds and capsules, which failed to perfect seeds.

De Vries has continued to find the recurrence of some of the mutants in the successive crops of seedlings of *Œnothera lamarckiana* indicative of the fact that the mutating period of the parent has not yet been passed. No departures from the parent type were found among the individuals which have come into bloom up to this time in the New York Botanical Garden.

The leaves of the seedlings of *Œ. lamarckiana* are easily distinguishable from those of *lata*, *nanella*, and *rubrinervis* even in the earlier stages, although not so easily separable from some of the other forms such as *brevistylis* and *leptocarpa* according to deVries. The earliest leaves were ovate, or round-ovate with rounded apices, or sometimes slightly pointed. These leaves as well as those formed at the age of five months were distinctly petiolate but with the laminæ relatively narrower. Adult basal

leaves of the rosette in the period immediately preceding flowering were petiolate with the apices bluntly pointed and with broad laminæ. The margins of all of the earlier leaves were sparingly but sharply toothed.

Plants set out early in May were blooming profusely early in August. The basal branches coming out from the axils in or near the rosettes were strong and vigorous but the upper branches of the stem were short and offered a distinct contrast to the longer, more slender branches of *rubrinervis*, with which it was also contrasted by its denser foliage and larger more showy flowers. Both stems and branches were thicker and heavier than in *rubrinervis*.

After noting the great variance in behavior and appearance of the parent and two mutants as described above, mature plants in bloom, the dried material of the younger plants, and photographs were submitted to Dr. J. K. Small, who had previously published an arrangement of the American species, and who is familiar with them in (Small, J. K. Œnothera and its Segregates. Bull. Torr. Bot. Club. 23: 167–194, 1896.) the herbarium and in the field. Dr. Small has kindly prepared the following statement concerning three forms, which is given in full below:

The characteristics of *Œnothera lamarckiana* and *Œ. rubrinervis* as given by Dr. Small are set in parallel columns for convenience of comparison:

Oenothera lamarckiana Ser.

I. *Seedling about two months old.*— Leaves sparingly pubescent; blades ovate to suborbicular, the larger about 2 cm. wide, obtuse or rounded at the apex, each abruptly narrowed into a petiole.

II. *Seedlings 5 months old.* — Rosettes relatively dense: leaves copiously fine-pubescent; blades typically oblong, the larger ones fully 3 cm. wide, quite approximately denticulate, obtuse, or somewhat apiculate at the apex, much longer than the petioles.

III. *Adult plant.* — Plant very stout and luxuriant, 0.5 to 1 m. tall. Stem markedly channeled, sparingly hirsute with rather spreading hairs, nearly simple, or with several relatively short ascending branches near the base, and few very short ones above: leaves very numerous, 2–2.5 dm. long about the base of the stem; blades shallowly and often irregularly toothed, those of the lower cauline leaves broadly spatulate to oblong, rather acute, each narrowed into a nearly semi-terete petiole, those of the upper cauline leaves oblong to oblong lanceolate, acute, or somewhat acuminate, short-petioled: bracts subcordate at the base: hypanthium 4.5–5.5 cm. long, about 8 mm. wide at the mouth, prominently ridged: sepals 4–5 cm. long, longer than the tubular portion of the hypanthium, the free tips 8–10 mm. long: petals firm 4–5 cm. long, emarginate: anthers 13–15 mm. long: stigmas 5–6.5 mm. long. (See Figs. 1, 4, 7 and 9.)

Oenothera rubrinervis deVries.

I. *Seedlings about 2 months old.* — Leaves manifestly less pubescent than those of *Oe. Lamarckiana*; blades elliptic, the larger ones about 1.5 cm. wide, acute or acutish at the apex, each gradually narrowed into a petiole.

II. *Seedlings 5 months old.* — Rosettes lax: leaves less densely pubescent than in *Oe. Lamarckiana*; blades spatulate to elliptic-spatulate or oblong-spatulate, the larger ones about 2.5. cm. wide, remotely denticulate, acute, or abruptly pointed at the apex, about as long as the petioles or shorter.

III. *Adult plant.* — Plant relatively stout, less luxuriant than *Oe. Lamarckiana.* Stem scarcely channeled, hirsute, with rather ascending hairs, typically branched throughout, the branches near the base elongated, decumbent, the upper ones gradually shorter: leaves numerous; blades less prominently toothed than in *Oe. Lamarckiana*, those of the lower cauline leaves spatulate to broadly oblong, obtuse or acutish, each narrowed into a relatively long petiole, those of the upper cauline leaves elliptic-oblong to oblong or oblong-lanceolate, acuminate, short-petioled: bracts rounded or round-truncate at the base: hypanthium 5.5 to 6 cm. long, about 4 mm. wide at the mouth, obscurely ridged: sepals 3.3 to 3.5 cm. long, shorter than the tubular portion of the hypanthium, the free tips 5–6 mm. long: petals tender, 3–3.5 cm. long, notched: anthers 6–10 mm. long. stigmas 7.5–10 mm. long. (See Figs. 2, 5, 8 and 10.)

Œnothera nanella was taken by deVries to have a degree of separation from the parent type that would lead it to be considered as a variety, a conclusion which is borne out by Dr. Small's description as given below:

I. *Seedling about two months old.* — Resembles that of *Œnothera lamarckiana*; but the leaf-blades are less uniform, some of them ovate or oval, others ovate and somewhat lobed near the apex, others broadly ovate, or prominently apiculate.

II. *Seedling 5 months old.*— Nearly like that of *Œ. lamarckiana*; but leaves inclined to have longer petioles.

III. *Adult plant.*— Plant, stout and stocky in all parts, resembling *Œ. lamarckiana*, but smaller, less than 3 dm. tall. Stem obscurely channeled, hirsute with somewhat ascending hairs, simple: leaves approximate, 7–12, 5 cm. long near the base of the stem; blades shallowly, often rather remotely, but quite evenly toothed, those of the lower cauline leaves spatulate to oblong, acute, or acutish, each narrowed into a semi-terete petiole, those of the upper cauline leaves broadly oblong to oblong-ovate, acute or slightly acuminate, nearly sessile: bracts subcordate at the base: hypanthium 3–3.5 cm. long, about 5 mm. wide at the mouth, obscurely ridged: sepals 3–3.5 cm. long, longer than the tubular portion of the hypanthium, the free tips 5–6 mm. long: petals 3.5–4 cm. long, emarginate: anthers 11–12 mm. long: stigmas 4–5 mm. long.

General Summary.

Discontinuous variation as a possible method of origin of species was considered by Charles Darwin in his studies of plants and animals under domestication, and he concluded that if new forms did arise in this way that they were not self-maintenant (1868). On the other hand Galton took the position that the evolution of species is not necessarily by minute steps (1889), but Dollo (according to deVries's, *Mutationstheorie*, Bd. 1, p. 46, 1901) was the first to accept discontinuous variation as the prevalent method of origin of species (1893). Bateson (1894) brought together a large amount of evidence as to types which have arisen in this manner, and a comprehensive summary of

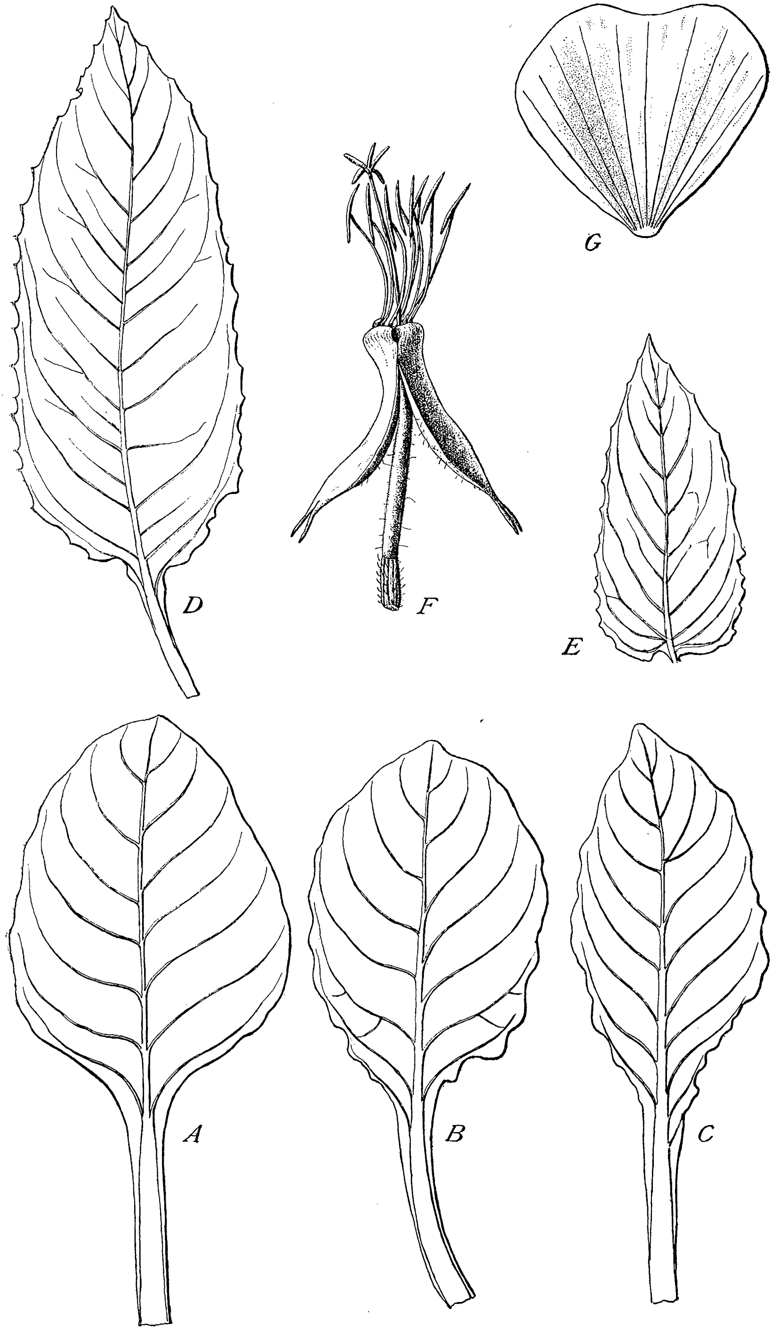

FIG. 9.—*Œnothera lamarckiana*. *A*, leaf from basal portion of adult rosette; *B*, leaf from middle, and *C*, leaf from upper portion of rosette; *D*, leaf from middle of flowering stem; *E*, bract from lower part of inflorescence; *F*, flower with petals removed; *G*, petal. (See Fig. 10.)

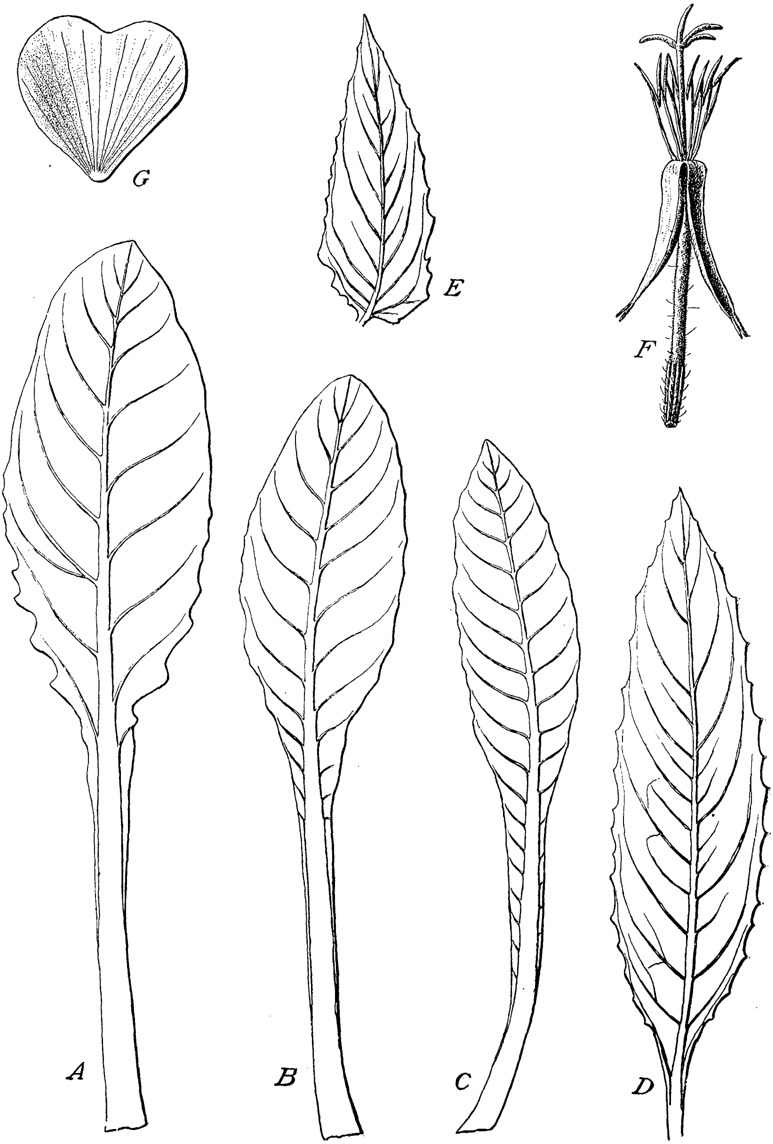

FIG. 10.—*Œnothera rubrinervis.* *A*, leaf from lower part of adult rosette; *B*, leaf from middle portion, and *C*, leaf from upper portion of rosette ; *D*, leaf from middle of flowering stem ; *E*, bract from lower part of inflorescence ; *F*, flower with petals removed ; *G*, petal. (See Fig. 9.)

the principal evidence furnished by plants was made by Korschinsky in 1899. Systematic observations upon the subject were begun by deVries in 1886 and have been continued until the present time. As a result of his investigations deVries formulated his "Mutationstheorie," which has appeared in book form, the separate parts of which have been published in the period of 1901–1903. This hypothesis rests upon the theory of pangenesis previously formulated by him.

The parent type, *O. lamarckiana*, from which deVries saw mutant forms arise has been found constant in its characters in cultivation in Europe and America and also when running wild. This type is not identical with any known member of the American flora, and is most nearly allied to *Onagra biennis grandiflora* (*Oenothera biennis grandiflora*) from which it is suggested it might have arisen by mutation.

The mutant derivatives of the parent form are found to be constant in their characters, with no connecting or intergrading forms, as illustrated by the cultures of the parent, *Œ. nanella* and *Œ. rubrinervis*, in the New York Botanical Garden during 1902–1903. The mutants are clearly separable from the parent and from each other both by physiological and taxonomic standards. Furthermore the specific character of the mutants was borne out by their behavior when hybridized with one another.

It has become evident from the results so far accomplished that the testing, study, proof or disproof of the theory of the origin of species by mutation involves an actual examination of lines of descent, and observations upon successive generations of organisms of known genesis. In this manner only may mutant forms be distinguished from hybrids, individuals with aberrant non-transmissible characters and teratological formations. The nature of the questions involved, and the essentially material character of the evidence to be considered is such that all controversial discussions not supported by facts of this character must be viewed with distrust. In no instance is this more plainly apparent than in the recent treatment of the subject by Vernon (Vernon, H. M. *Variation in Animals and Plants*. 1903). This author says "Hence it (*Œnothera lamarckiana*) is probably a garden variety of *Œnothera biennis* (Evening Primrose), and

may be a hybrid plant, whilst the mutations obtained by deVries may be merely partial or complete reversions to the original ancestors of the plant." It is quite possible, and even probable that *Œ. lamarckiana* may have been originally derived from the same type as *Œ. biennis* as noted above, but to designate it as a "garden variety," and as such ineligible as research material is simple evasion. The plant in question has been under more or less continuous observation for a hundred and fifteen years during which period it has been constant in its characters, and has shown no evidence by anatomical similarity or physiological behavior of being anything but an independent species. With what species could *biennis* hybridize to produce *lamarckiana*? The genus comprises a comparatively small number of types, all natives of America, and none of which were available as a hybrid mate to *biennis* at the time of the origin of *lamarckiana*. The conjecture in question is totally unsupported after the most rigid search for evidence upon the matter.

Again to consider the mutants as reversions to the original ancestors of *lamarckiana* is impossible, since the mutant forms exhibit qualities not possessed by any other known members of the genus, including *biennis*.

The point raised by Bateson and Saunders (Reports to the Evolution Committee. Royal Society. I. p. 153, London, 1902) that the pollen of *lamarckiana* contains deformed grains, which points to its origin by crossing, is without significance, since the author has found that the stamens of plants of *biennis* growing in the vicinity of New York exhibit a much larger proportion of deformed pollen than that of the specimens of *lamarckiana* cultivated in the New York Botanical Garden.

It has been impossible so far to assign mutations to definite causes, or to forecast the frequency, or occurrence of the phenomenon. These phases of the subject constitute the most important problems of the subject, which await investigation. Theoretical evidence upon such a subject can have but limited value, and conclusions of any satisfactory degree of finality may be expected only from direct experimental research under circumstances in which the probability of error is reduced to a minimum.

So far as the origin of mutations is concerned, it seems well decided that the premutative alterations in seed-plants ensue in the vegetative and sexual cells previously to the formation of the embryo in which they first appear, and that no environmental disturbances may bring about the alterations in question by direct action on the seedling.

It is not the purpose of this paper to discuss the various theories which have been put forward from time to time to account for the origin of species, but to bring under consideration the facts upon which the conclusions as to the origin of species by discontinuous variation have been based by deVries. These facts make inevitable the conclusion that new types of specific rank, taxonomically separable, and physiologically distinct and constant, without intergrading and connecting forms, have arisen in Œnothera by discontinuous variation. That mutation is the principal method of evolutionary procedure is not proven. That natural selection is universally prevalent is certainly disproven: that natural selection or any other method is capable of accounting for the existence of any single species has not been proven with the finality offered by the evidence of discontinuous variation. It may be said, therefore, that species have actually been demonstrated to have arisen by mutation, some are known to have arisen as the result of hybridization, and that evidence has been accumulated which has been interpreted to demonstrate the origin of species by natural selection, and by adaptation. Nothing in the nature of living organisms demands that all species should have originated in the same manner, or that one simple, or single method of procedure should have been followed.

NEW YORK BOTANICAL GARDEN,
August, 1903.